A trait-based approach to crop–weed interactions

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A trait-based approach to crop-weed interactions

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Running head: Trait-based crop-weed interactions

Abstract

Understanding the mechanisms of community assembly may provide evidence to improve crop management, and in particular how weeds impact on crop yields. Focussing on plant functional traits and their diversity, we analysed a crop-weed interaction study with different levels of weed species and barley cultivar diversity to assess how weed species and barley cultivars respond to competition. Pre-emption of light resources by the taller barley did not impact on the weeds, with both weeds and barley showing similar order of magnitude shifts in height, specific leaf area and leaf dry matter content in response to crop-weed competition. These shifts were to a more conservative growth pattern, and suggest in this study a greater importance of below- than above-ground interactions in driving trait responses. The mixture of barley cultivars shifted the weeds to a more conservative growth pattern compared to the cultivar monocultures. The results indicate that cultivar mixtures could result in less need for weed control in arable fields, and possibly that the development of complementary cultivar mixtures could reinforce this effect. This confirms the results of other studies which show that mixtures either improve yields or make yields less variable in response to weed competition.

Highlights

1. We analysed how traits were modified in a crop-weed interaction study

2. Pre-emption of light resources by the taller barley did not impact on the weeds

3. Weeds shifted to a more conservative growth pattern in competition with barley

4. A mixture of barley cultivars altered weed traits further than monocultures

Keywords: Arable weeds, barley, competition, functional diversity, plant community assembly, plant functional traits, weed control

52 1. Introduction

53

54 Food security remains a significant global problem, with, for instance, 12.5 % of the world's
55 population undernourished in terms of energy intake (FAO 2013). Improvement in
56 agricultural productivity is part of the solution to this problem and one part of that
57 productivity gain could be achieved through strategies to alter the balance of crop-weed
58 competition (Oerke & Dehne 2004). Understanding plant-plant interactions has been a
59 major focus of ecology (Brooker 2006; Callaway & Walker 1997), and latterly a functional
60 approach to these interactions has been formulated (Violle & Jiang 2009). Such ecological
61 knowledge could be applied to agriculture to generate a functional understanding of crop-
62 weed interactions, and this understanding could be used to improve the management of
63 arable systems.

64 Functional response traits (i.e. traits that underpin species responses to
65 environmental conditions) can be used to understand the response of vegetation to
66 changing management (Díaz *et al*. 2007; Garnier *et al.* 2004) or to environmental conditions
67 (Kleyer *et al.* 2012; Pakeman *et al.* 2009). Plant functional response traits can also shed light
68 on the processes of community assembly to understand the role played by abiotic filtering
69 and biotic interactions in structuring vegetation (Shipley *et al*. 2006; Kraft *et al*. 2008; Schöb
70 *et al*. 2012) as these traits can be seen as describing a species' niches (Violle & Jiang 2009).
71 The development and application of these approaches has largely focussed on natural
72 vegetation communities, but there is an opportunity to use them to understand plant-plant
73 interactions in arable cropping systems in order to refine management to boost yields or
74 protect biodiversity by reducing pesticide use (Gunton *et al*. 2011; Schellberg & Pontes
75 2012).

To understand how plant-plant (e.g. crop-weed) interactions control the dynamics of communities over space and time, intra-specific shifts in trait values need to be studied (Berg & Ellers 2010). There is evidence that trait variation can result from species interactions within plant communities (Valladares *et al.* 2006). It is thought that - by reducing niche overlap - shifts in trait value promote species coexistence and hence diversity in natural communities (Callaway *et al.* 2003). Such a focus has contributed to understanding the mechanisms of community assembly within (semi-) natural communities (Jung *et al*. 2010; Mason *et al.* 2011; Hulshof *et al*. 2013). Although the importance of intra-specific variation in arable plants has been recognised, both in terms of traits that facilitate the persistence of arable weed species (Hawes *et al*., 2005; Iannetta *et al.*, 2007; Storkey *et al*., 2010) and the productivity of crops in the presence of weeds (Davis *et al*. 2004; Hoad *et al*., 2008; Walker *et al.* 1990), little attempt has been made to apply a trait-based approach to explore the vegetation dynamics of arable plant communities (Navas 2012). This study applies a trait-based approach to quantify and interpret the effect of crop-weed interactions on the expression of crop and weed traits. In particular, it focusses on the use of within-species genetic mixtures of crops as one method to improve the sustainability of crop production as there is evidence that genetic mixtures are more resilient to environmental variation (Newton *et al.* 2009; Kiær *et al.* 2012) and exhibit greater weed suppression compared to crop cultivar monocultures (Kiær *et al.* 2009). The premise of this paper is that examining trait responses to understand how plants (crops and weeds) in arable systems respond to competition will contribute to understanding the benefits of crop genetic (cultivar) mixtures, which in turn would contribute to improving agricultural sustainability (Frison *et al.* 2011). In particular it focusses on trait responses that indicate shifts in competitiveness or changes in niche position or breadth as possible indicators of crop-weed

100 interactions. The degree to which trait plasticity can alter plant-plant interactions in arable
101 systems is little studied although its importance in cereals (Peltonen-Sainioa *et al*. 2011) and
102 barley variety mixtures in particular has been noted (Newton & Swanston 2004).

103 Using constructed crop-weed communities, the objectives of this study were, firstly,
104 to quantify crop and weed traits relevant to analyse crop-weed interactions (Hoad *et al*.,
105 2008; Storkey *et al*., 2012) in single cultivar/species vegetation stands and, secondly, to
106 assess the impact of crop-weed competition on the values of these traits in mixed
107 cultivar/species vegetation stands. We selected traits that were both informative with
108 regard to plant responses to the environment and rapid to measure given the scale of the
109 experiment (Pérez-Harguindeguy *et al.* 2013). Predictions based on previous work would
110 indicate differences in response between weeds and crops because of the higher variability
111 in the traits expressed by the different weed species compared to that between the barley
112 cultivars (Cahill *et al.* 2008). Similarly, from the results of Hoad *et al.* (2008) it would be
113 expected that the taller barley may pre-empt resources (light), and thus significantly impact
114 on the weed community. Furthermore, the work of Heikkinen & Mäkipää (2010) suggests
115 that a mixture of barley cultivars may impact the weed community more than individual
116 cultivars through greater niche filling. We tested the following hypotheses: (1) Barley
117 cultivars are less responsive to growing with other cultivars than weed species growing with
118 other weed species because competitive effects are less variable intraspecifically (i.e.
119 between cultivars) than interspecifically (i.e. between species). (2) As plant height is a key
120 effect trait it is important in competition for light (Navas & Violle 2009), and as barley is
121 generally taller than many common arable weeds, the taller barley will show less trait
122 plasticity than the shorter weed species in response to crop-weed competition. (3) The
123 barley cultivar mixture will have a greater impact on weed species traits than individual

124 barley cultivars because of its greater occupation of niche space and hence result in reduced
125 niche space for the weeds. (4) Trait shifts within the weed community or in the barley
126 mixtures in response to competition will be accompanied by a reduction in trait variability as
127 less ‘trait-space’ is available for exploitation at the community level due to niche space
128 consumption by competitors.
129

2. Material and Methods

Full details of this experiment are published in Schöb *et al.* (2015) which assessed the performance responses of the barley cultivars and weed species alone and in mixtures.

2.1 Mesocosm construction and treatment

Artificial mesocosm communities were constructed in a greenhouse at the James Hutton Institute in Aberdeen (UK, 57° 8’ 6’’N, 2° 9’ 24’’W). Communities were randomly allocated to mesocosms and established in soil-filled boxes measuring 0.7 m x 0.7 m (approximate surface area of 0.5 m^2) and boxes were filled to a depth of 0.3 m. Boxes were constructed of wood, lined with thick plastic, and filled with homogenised loam topsoil over a roughly 5 cm deep layer of gravel. Mesocosms were kept under natural daylight, received no fertiliser additions, but were watered with equal amounts of water on a regular basis. Air temperature and relative humidity were not controlled and varied between 5-25 °C and 40-100 %, respectively.

Pre-germinated seedlings of barley and arable weeds (see below for details) were planted in the mesocosms between 6 and 14 June 2012, except for the barley cultivar Oxbridge (19 June) and *Euphorbia helioscopia* (18 July) which exhibited low germination rates. Prior to planting all seeds were soaked overnight in 1 µM gibberellic acid (Sigma-Aldrich Chemie GmbH, Steinheim, Germany) aqueous solution, spread on standard commercial seedling compost and germinated in a growth room maintained for the first two days under dark conditions and at 5 °C. Weed seedlings were then grown in the greenhouse under ambient temperature and daylight conditions for a further 3 weeks. Barley seedlings

were grown for only one further week prior to planting under growth room conditions at 20/18 °C and with a 12 hour day/night regime.

Mesocosms were monitored twice a week for survival, health and developmental status. To prevent lodging, the tops of all barley plants were gently wafted with a wooden stick five times a week for 10 weeks after planting (a common technique when growing barley and other cereals in greenhouse conditions). To limit mildew and aphid infestation, all plants were treated with a fungicide (ALTO 100 SL, Syngenta Crop Protection Inc., Greensboro, USA; active ingredient: cyproconazole) and soap (SAVONA, Koppert B.V., AD Berkel en Rodenrijs, NL; active ingredient: fatty acids) at 30 and 80 days after planting. Trait measurements were initiated 55 days after planting the first seedlings, except for Oxbridge (50 days) and *E. helioscopia* (20 days).

2.2 Diversity treatments

A standard planting density of 60 plants per mesocosm was used for all treatments. Each mesocosm box was divided into 64 equal square cells, and the seedlings planted in the centre of each cell. Equal proportions of each cultivar or species in mixtures were randomly allocated one to each grid squares, leaving empty four squares per mesocosm box.

Communities were assembled using different combinations of five barley cultivars (Optic, Oxbridge, Sebastian, Tipple, and Westminster) and five weed species commonly found in barley crop fields in the UK: *Capsella bursa-pastoris* (L.) Medik. (Brassicaceae), *Euphorbia helioscopia* L. (Euphorbiaceae), *Poa annua* L. (Poaceae), *Senecio vulgaris* L. (Asteraceae) and *Stellaria media* (L.) Vill. (Caryophyllaceae). Barley seeds were obtained from seed stocks held at the James Hutton Institute (Dundee, UK) except Sebastian, which

was obtained from Sejet Plant Breeding (Horsens, Denmark). Weed seeds were supplied by Herbiseed (Twyford, UK). Nitrogen-fixers were excluded so as to reduce the complexity of interactions. All cultivars and species were grown in monoculture - 1B (barley), 1W (weed), 10 treatments - and in mixtures of either all five barley cultivars with no weeds (5B, 1 treatment, 12 plants per barley cultivar), all five weed species and no barley (5W, 1 treatment, 12 plants per weed species), one barley cultivar and five weed species (1B5W, 5 treatments, 10 plants per cultivar or weed species), and five barley cultivars and five weed species (5B5W, 1 treatment, 6 plants per cultivar or weed species). There were four replicates of each treatment. This resulted in 18 different species x cultivar combinations and 72 plots in total. It is important to note that our design is not fully-factorial due to logistical constraints; specifically the design meant that barley mixtures containing only a single weed species were not examined. This determined the statistical comparisons we could make (see below).

2.3 Trait measurement

Three traits were selected for measurement: height is correlated to competitive ability for light, Specific Leaf Area (SLA) is a measure of a plant's strategy for light capture and Leaf Dry Matter Content (LDMC) a measure of its carbon investment strategy (Garnier *et al.* 2004). Traits were measured in order of the mesocosms in the greenhouse (with the last mesocosm measured 14 days after the first mesocosm) and for 5 randomly selected individuals of each weed species or barley cultivar within each mesocosm. For trait measurements we followed the protocol by Pérez-Harguindeguy *et al.* (2013). Plant height was measured as the distance between the uppermost tip of photosynthetic tissue and the

ground level. For Specific Leaf Area (SLA) and Leaf Dry Matter Content (LDMC) we carefully removed a fully developed and healthy leaf of each plant individual, fully rehydrated the leaf overnight and measured fresh mass and leaf area. After drying the leaf at 80 °C for 48h we determined dry mass. SLA was then calculated as the ratio between leaf area of the fresh leaf and leaf dry mass (mm^2 mg^{-1}) and LDMC as the ratio between leaf dry mass and fully rehydrated fresh mass (mg g^{-1}).

As some traits like height are linked to performance, there is an issue with assessing the impact of competition on them: for instance, it is not possible for a poorly performing plant to be tall. Consequently, an allometric correction was applied to the height data to account for this. In effect this measure becomes a measure of height allocation relative to biomass. Corrections were made by dividing height by (above-ground biomass)$^{0.25}$ (Enquist 2002); biomass methods specified in Schöb et al. (2015).

Apart from mean traits per barley cultivar or weed species, two measures of functional diversity (FD) were calculated for these traits individually in order to assess shifts in the variability of the traits expressed by the barley and weeds between treatments. Functional richness (FRic) was used to assess the range for single traits and the convex hull of points in trait space for the multi-trait measure (Cornwell *et al.* 2006). To assess trait dispersion of a species, Rao's (1982) measure of quadratic entropy (Botta-Dukát 2005):

$$RaoQ = \sum_{i,j}^{S} d_{ij} p_i p_j$$

where S is the total number of species in the community, d_{ij} is the difference between the i-th and j-th species and abundances were set to one to reflect the experimental frequency of each individual. Calculations of FRic and RaoQ were carried out using *FD* (Laliberté &

223 Legendre, 2010; Laliberté & Shipley, 2011) in *R* version 2.12.1 (R Development Core Team,
224 2010).
225
226 2.4 Statistical analysis
227
228 Hypothesis 1 (H1) was tested by comparing the impact of diversity on the traits of barley
229 cultivars and weed species; specifically by comparing diversity treatments (1 or 5 cultivars, 1
230 or 5 species) and their interaction with whether the mixture consisted of weeds or barley.
231 No mixtures containing both weeds and barley were included in this analysis. The random
232 model was taxon (barley cultivar or weed species) nested within mesocosm (and this held
233 also for H2 and H3, below). A subsidiary test (H1b) was made to assess if taxa behave
234 differently within the groupings (weeds or barley) by assessing if the interaction between
235 diversity and taxon identity was significant. H2 was tested by comparing the impact of
236 growing in mixtures on the mean traits and FD of the barley and the weeds; specifically by
237 comparing the 1B and 5W treatments with the 1B5W treatment. A subsidiary test (H2b)
238 focussed on the impact on individual taxa as opposed to the overall response of the barley
239 or weeds. H3 addressed how the number of barley cultivars present affected the mean
240 traits of weed species in general; 5W v 1B5W v 5B5W. H3b assessed the impact on
241 individual taxa. Finally, H4 was addressed by testing the shifts in mean traits and FD values
242 across the whole community; for barley by comparing across weed community
243 presence/absence (1B v 5B x 0W v 5W), and for weeds by comparing across barley diversity
244 (5W v 1B5W v 5B5W). The impacts on traits of individual cultivars and of individual species
245 were also tested. The random model, as this addressed community level values, was just
246 mesocosm.

247 Statistical analysis was carried out within *nlme* (Pinheiro *et al.* 2010) in *R* version
248 2.12.1 (R Development Core Team, 2010), with results where $p < 0.1$ reported. Differences
249 between taxa in variables such as height and SLA are expected. These are noted in the
250 tables but not discussed in the text.

3. Results

3.1 H1. Barley cultivars respond less to other cultivars than weeds to other weed species

The analysis of purely barley cultivar or weed species mixtures (i.e. excluding weed-barley combinations) showed no effect of diversity treatment on the height of the barley or weeds (Table 1a, Figure 1a). However, when allometrically adjusted for performance, there was a significant interaction between diversity and plant identity (i.e. barley or weed): the (adjusted) height of weeds increased when grown in a mixture of weeds, but that of the barley decreased when grown in a mixture of barley cultivars (Figure 1b). The mean absolute change was higher for the weed species (40.9 %) compared to the barley cultivars (5.7 %).

These overall patterns hid differences in responses between species and cultivars (H1b), as indicated by significant diversity x taxon interaction terms, particularly for the allometrically adjusted height (Table 1b). The weeds *Euphorbia*, *Poa* and *Senecio* responded to being in a weed mixture by growing taller, whilst *Capsella* and *Stellaria* responded with a shorter stature (Figure 1b), indicating different impacts of the shade avoidance response of etiolation on the morphology of plants with different growth forms. The barley cultivars Optic, Sebastian and Tipple were shorter when grown with other barley cultivars, whilst Oxbridge and Westminster showed no response (Figure 1b). The taxon-specific height responses were accompanied by similar responses in the variance of plant heights (Table 1b). The weeds *Euphorbia*, *Poa* and *Senecio*, when in weed mixtures, displayed greater height variance - measured as FRic (Figure 1c) or Rao's Q (Figure 1d) - whilst *Capsella* and *Stellaria* were less variable, possibly relating to their different shade avoidance strategies

(see above). All the barley cultivars showed reduced height variance when grown with other cultivars, except for Oxbridge, which showed no difference in height variability when grown alone or with other cultivars.

The impact on height diversity of growing with other taxa was higher for the weeds (FRic 70.5 % mean absolute change, Rao's Q 209.2 %) than for barley (20.5 % and 33.9 % respectively). Variability in SLA increased in the weeds when grown as a mixture, irrespective of whether it was measured as FRic (Figure 1e, mean absolute change 28.9 %) or Rao's Q (Figure 1f, 61.9 %), but decreased for the barley (25.0 % and 40.9 % respectively). However, there was no significant interaction between taxon and diversity, nor was there an interaction effect on the community-weighted mean of SLA and LDMC, and the variability of LDMC.

3.2 H2. Taller barley will show less trait plasticity than shorter weed species in response to crop-weed competition

Analysis of the combined weed and barley mixtures (Table 2) showed that, not surprisingly, barley and weeds differed in their (absolute and adjusted) heights, but also that this effect was not dependent on whether the plants were growing in monocultures or in a barley-weed mixture (Table 2a, Figure 2a, 2b). Consequently neither group's height was particularly responsive to the barley-weed mixture treatment.

Analysis of absolute height indicated no taxon-specific responses: there was a significant impact of the barley-weed mixture treatment, with a slight overall decrease in height for all taxa when grown in mixtures, but no mixture x taxon interaction (Table 2b). However, for allometrically adjusted height not only did a similar general reduction occur

for all taxa in mixtures, there was also a weak interaction between taxon and the mixture treatment (Table 2b). Some taxa showed a slightly greater responsiveness, and in particular there were larger height reductions for Sebastian and Tipple, and even small height increases for *Capsella* and *Stellaria* (Figure 2b). The mean absolute impact on allometrically adjusted height of growing in the mixtures was similar for the weeds and the barley (5.6 % and 7.4 %, respectively).

Although there were overall differences in SLA and LDMC values of the barley and weed groups, these differences were not influenced by growth in mixtures (Table 2a). However, when analysed at a taxon rather than group level, both SLA (Figure 2c) and LDMC (Figure 2f) were significantly affected by growing in mixtures. Both traits had overall lower values in the mixtures, although the lack of significant mixture x taxon interactions terms for SLA and LDMC (Table 2b) indicated that this effect was consistent across taxa. There was little difference in the mean absolute impacts of competition on these traits for the barley (SLA 7.1 %, LDMC 5.2 %) and the weeds (4.6 % and 2.2 % respectively).

For SLA, FRic and Rao's Q was overall lower for barley than for weeds (Table 2a) and differed between taxa (Table 2b). The was a significant effect on these variables of the barley-weed mixture treatment, but lack of significant mixture x barley/weeds or taxon interaction terms indicated that the mixture treatment reduced variability of SLA to a similar extent for all taxa. There was no effect on the variability of either height or LDMC for both barley and weeds when growing in the barley-weed mixture, nor any mixture x barley/weeds or taxon interaction effects (Table 2).

3.3 H3. The barley cultivar mixture will have a greater impact on weed species traits than individual barley cultivars

The response of the weed species to increasing barley diversity (no. of barley cultivars within a mixture) was restricted to the two leaf traits, SLA and LDMC (Table 3a). As the diversity of the barley increased, on average the SLA of the weed species declined (Figure 3a). Averaged across species, the absolute impact of adding one cultivar was 2.2 %, but of adding five it was 10.8 %; the effect consequently appears additive. LDMC showed a positive overall response to increasing barley diversity with a mean absolute impact of adding one barley cultivar at 4.6 and of adding five cultivars 8.0%; for this trait the effect seems logarithmic rather than additive. The significant cultivar no. x species interaction term indicated differences in the levels of responsiveness between species: *Euphorbia* was the most sensitive species, and *Senecio* and *Stellaria* the least.

None of the traits of the weed species showed variation in response depending on the individual barley cultivars with which the weeds were growing (Table 3b).

3.4 H4. Trait shifts in response to competition will be accompanied by a reduction in overall trait variability

For barley, the presence of weeds had overall a weak impact in terms of reducing allometrically adjusted height (Table 4ai, Figure 4a). However, there was also evidence of differences in this response between cultivars (Table 4aii), with large decreases for Sebastian and Tipple, but little effect on Optic and Oxbridge and on the five cultivar mixture. Similarly, adding weeds significantly reduced overall barley SLA (Table 4ai, Figure 4b), and again there were significant differences in the response of different cultivars (Table 4aii). Optic, Oxbridge and Tipple had lower SLAs when grown with the weeds, whilst the five

347 cultivar mixture and Westminster remained stable and Sebastian showed an increase
348 (Figure 4b). There was weaker evidence that the variability in barley SLA declined when
349 grown with weeds (Figure 4c). LDMC was not affected by the presence of weeds in this
350 study.

351 For the weed community as a whole, the presence of barley reduced SLA (Table 4b,
352 Figure 5a), and there was an indication that, when grown with the full barley mixture, weed
353 LDMC was higher (Figure 5b). There was no impact of the number of barley cultivars present
354 on the height of the whole weed community, and adding barley had no impact on the
355 variability of height, SLA or LDMC of the whole weed community.

356 4. Discussion

357

358 It was clear that the barley cultivars were less responsive to growing in a mixture of cultivars
359 in terms of height changes, height variability and SLA variability than the weed species when
360 grown with other weed species. Also, the responses differed in direction, with the barley
361 cultivars generally showing reduced height and reduced variability when grown with other
362 cultivars whereas the weed species showed increased height and variability when grown
363 with other weeds. Trait responses can be interpreted as indicators of the interactions
364 occurring between the harvested, focal plant and its neighbours. Thus it is clear that the
365 presence of neighbours of different cultivars rather than the same cultivar means little for
366 the barley cultivars in terms of their plant-plant interactions, but that the occurrence of
367 different species rather than con-specifics has a considerable impact on a number of the
368 weed species. In barley the mean trait changes are subtle (as the neighbours are still the
369 same species), whereas for the weeds, as the neighbouring species are very different in
370 growth form and mean traits, then larger changes in trait means were observed. Thus
371 Hypothesis 1, that barley cultivars will be less responsive to growing with other cultivars
372 than weeds species with other weed species, was supported for the traits investigated.

373 Despite our expectations (H2), the taller barley showed very similar levels of height
374 plasticity as the weeds when barley and weeds were grown together, with generally small
375 reductions in height. There was similarly little impact of growing together on mean SLA or
376 mean LDMC for either the weeds or the barley, whereas growing in a mixture reduced the
377 variability in SLA regardless of taxon. Hypothesis 2, that the taller barley will show less trait
378 plasticity than the shorter weed species in response to crop-weed competition, is not
379 supported. All barley cultivars in fact showed reduced variability in SLA when grown in a

mixture with weeds, whilst variability in SLA in the weeds was unaffected by the presence of barley.

For the traits of the weed species that showed a response to barley, the response was bigger when five barley cultivars were present than when only one was present. Thus SLA was reduced more on average by the presence of a diverse mixture of barley cultivars than by the presence of only one, whilst LDMC increased more with a diverse mix of cultivars. This suggests that the five cultivar mixture shifts individual weed species (Figure 3) and the weed community (Figure 5) into a more conservative pattern of leaf investment (Grime et al. 1997; Wright et al. 2004), which implies that the response of the weeds to competition will make them less competitive over the short-term (Violle *et al.* 2009). It also implies that, whilst individual barley cultivars have similar effects on the weeds, each barley cultivar is occupying subtly different niches and that this seems to be an additive effect. It is also an effect that appears not to influence the between cultivar interactions. However, certain species were more plastic, such as *Capsella* and *Euphorbia*, so this effect may differ depending on the composition of the weed community. These results suggest support for Hypothesis 3; the barley cultivar mixture will have a greater impact on weed species traits than individual barley cultivars and hence suggests that cultivar mixtures are potentially of use in reduced input agriculture.

Despite shifts in a number of trait averages, there was very little evidence to suggest that more complex competitive interactions resulted in a reduction in trait space available for individual taxa. The exception to this was that the variability in SLA reduced for the barley cultivars when grown with weeds. This suggests that there is little evidence to support hypothesis 4, that trait shifts in response to competition will be accompanied by a reduction in trait diversity as less 'trait-space' is available for exploitation by the weeds

404 because of the presence of barley and vice versa. The implication of this is that cultivating
405 mixtures of cultivars may reduce the performance of competing weeds, but would not
406 impact on weed community assembly or diversity.
407
408 The interactions between the crop plant (barley) and the weeds resulted in a general shift
409 towards more resource conservative growth (reduced allometrically adjusted height,
410 reduced SLA, increased LDMC) for both the barley and weeds. This is indicative of reduced
411 resource availability, potentially light, soil nutrients or water, shifting the plants towards a
412 more conservative growth strategy that is less likely to result in rapid growth (Ordoñez *et al*.
413 2009, Poorter *et al*. 2009, Pérez-Harguindeguy *et al*. 2013). This reduction in available
414 resources could come from increased complementarity of growth strategies as a result of
415 increasing niche overlap (Mason *et al.* 2011), which could have resulted in the reduced trait
416 variability expressed for SLA. There were some exceptions to this, *Capsella* and *Stellaria*
417 showed increased heights in the mixture, *Senecio* increased SLA and *Euphorbia* decreased
418 LDMC. However, no taxon showed any consistency (i.e. increased height and SLA, and
419 decreased LDMC) in response to competition, except for Sebastian, which showed increased
420 SLA and decreased LDMC. This finding suggests that this cultivar may be more effective in
421 weed suppression than the other cultivars as it responds to weed competition by a more
422 short-term investment strategy; indeed, in both the 1B5W and the 5B5W Sebastian was the
423 best performing cultivar (Schöb *et al.* 2015).
424 Interestingly, from an agronomic viewpoint, the trait shifts in the weeds were
425 amplified when the number of barley cultivars was increased to five. The more cultivars
426 present, the more conservative the growth strategies of the weeds. This finding suggests
427 that there is some complementarity between the barley cultivars and hence greater niche

space usage that prevents the weeds from exploiting resources in the same way as when only one cultivar is present. This is reflected in the (although weak) complementarity effects on yield from increasing crop cultivar diversity in this experiment (Schöb *et al.* 2015). However, this is not evident from the analysis of the three traits in this paper, which suggests that the key interactions within this system are below-ground competition for nutrients and/or water (Kiær *et al.*2013; Wilson 1988), particularly as root volume is limited in the experimental set up. In contrast, light competition should result in increased SLA to aid foraging (Gutschick & Wiegel 1988; Valladares& Niinemets 2008), whilst a shift to higher LDMC reflects a strategy for coping with reduced nutrient or water availability (Pakeman 2013). This shift towards more conservative growth strategies with a high diversity crop mixture could be exploited, as it should result in less seed production by the weeds (and hence smaller seed bank contributing to future populations) and less yield reduction in the crop; which is the case in this experiment (Schöb *et al.* 2015). This latter is consistent with the barley cultivars showing relatively little response to being grown with genetically different neighbours of the same species. However, as cultivars do not all behave in the same way there is the possibility that complementary cultivars could be identified that have the biggest cumulative impact on the weed community.

This study of crop-weed interactions highlights the complexity of plant responses in mixed communities. Interestingly the hypothesis of the taller barley pre-empting light resources and hence affecting the weeds was not supported and, in fact, there was greater reduction in niche space (expressed as variability in SLA) for the barley cultivars. This suggests that the patterns observed by means of leaf traits above-ground may be a response to competition for resources below-ground – the more conservative growth patterns were probably a

response to reduced nutrient availability, whereas reduced light availability should have led to higher SLA values for the weeds. However, the most interesting result is that the high diversity mix of barley cultivars shifted the weeds to a more conservative growth pattern compared to the cultivar monocultures. This suggests that the development of cultivar mixtures could result in less need for weed control whilst at the same time improving yields (Schöb *et al.* 2015). Similar approaches have been shown to work in grasslands, where mixtures yielded more than monocultures and were more resistant to weed invasion (Finn *et al*. 2013).

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462

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Table 1. Results (p values from linear mixed models, where $p < 0.1$) from testing the impact of diversity on the trait means and functional diversity of barley cultivars and weed species (Hypothesis 1). (a) Comparing diversity treatments (1 or 5 cultivars; 1 or 5 species) and their interaction with whether the taxon is a barley or weed. (b) Assessing the impact on individual taxa (H1b, cultivars of barley or species of weeds). No barley-weed mixtures were included in this analysis (see Table 2 for these results). The random model was taxon nested within mesocosm. Abbreviations: FRic functional Richness; LDMC Leaf Dry Matter Content; SLA Specific Leaf Area.

(a)	Diversity	Barley v Weed	Diversity x Barley/Weed
Height		<0.001	
Allometrically adjusted height		< 0.001	0.028
Height FRic			
Height Rao's Q			
SLA		< 0.001	
SLA FRic		<0.001	0.009
SLA Rao's Q	0.039	<0.001	0.026
LDMC		0.002	
LDMC FRic			
LDMC Rao's Q			

(b)	Diversity	Taxon	Diversity x Taxon
Height		< 0.001	0.078
Allometrically adjusted height		< 0.001	0.003
Height FRic		0.083	0.026
Height Rao's Q			0.032
SLA		< 0.001	
SLA FRic		<0.001	
SLA Rao's Q	0.035	<0.001	
LDMC		< 0.001	
LDMC FRic		0.004	
LDMC Rao's Q			

644 Table 2. Results (p values from linear mixed models, where $p < 0.1$) from comparing the
645 impact of growing in mixtures of barley combined with weeds on the trait means and
646 functional diversity of the barley and the weeds (Hypothesis 2). (a) Comparing barley versus
647 weeds, and (b) the impact on individual taxa (H2b, barley cultivars or weed species). The
648 random model was taxon nested within mesocosm. Abbreviations: FRic functional Richness;
649 LDMC Leaf Dry Matter Content; SLA Specific Leaf Area.

650

651

(a)	Mixture	Barley v Weeds	Mixture x Barley/Weeds
Height		<0.001	
Allometrically adjusted height		<0.001	
Height FRic		0.022	
Height Rao's Q		0.026	
SLA		<0.001	
SLA FRic	0.013	<0.001	
SLA Rao's Q	0.045	<0.001	
LDMC		<0.001	
LDMC FRic			
LDMC Rao's Q			

(b)	Mixture	Taxon	Mixture x Taxon
Height	<0.001	<0.001	
Allometrically adjusted height	<0.001	<0.001	0.075
Height FRic		<0.001	
Height Rao's Q		<0.001	
SLA	<0.001	<0.001	
SLA FRic	0.010	<0.001	
SLA Rao's Q	0.038	<0.001	
LDMC	<0.001	<0.001	
LDMC FRic		<0.001	
LDMC Rao's Q		0.003	

652

653

Table 3. Results (p values from linear mixed models, where $p < 0.1$) from assessing (a) how the number of barley cultivars present affected the mean values and functional diversity of traits of individual weed species (Hypothesis 3) and (b) how individual barley cultivars affected the same. The random model was taxon nested within mesocosm. Abbreviations: FRic functional Richness; LDMC Leaf Dry Matter Content; SLA Specific Leaf Area.

(a)	Cultivar No.	Species	Cultivar No. x Species
Height		<0.001	
Allometrically adjusted height		<0.001	
Height FRic		<0.001	
Height Rao's Q		<0.001	
SLA	0.042	<0.001	
SLA FRic		0.002	
SLA Rao's Q		0.003	
LDMC	0.090	<0.001	0.019
LDMC FRic		<0.001	
LDMC Rao's Q		<0.001	

(b)	Cultivar	Species	Cultivar x Species
Height		<0.001	
Allometrically adjusted height		<0.001	
Height FRic		<0.001	
Height Rao's Q		<0.001	
SLA		<0.001	
SLA FRic		0.004	
SLA Rao's Q		0.005	
LDMC		<0.001	
LDMC FRic		<0.001	
LDMC Rao's Q		<0.001	

Table 4. Results (p values from linear mixed models, where $p < 0.1$) of assessing the shifts in trait means and functional diversity values across the whole community for (a) barley by comparing across (i) weed community presence/absence and (ii) for individual cultivars interacting with weed presence/absence, and for (b) the weed species by assessing the impact of (i) barley diversity and (ii) specific cultivars. The random model was mesocosm. Abbreviations: FRic functional Richness; LDMC Leaf Dry Matter Content; SLA Specific Leaf Area.

(a)	(i) Weeds	(ii) Weeds	Cultivar	Weeds x Cultivar
Height				
Allometrically adjusted height	0.056	0.025	0.008	0.075
Height FRic				
Height Rao's Q				
SLA	0.051	0.016	0.005	0.015
SLA FRic				
SLA Rao's Q	0.057	0.057		
LDMC				
LDMC FRic				
LDMC Rao's Q				

(b)	(i) Barley Diversity	(ii) Cultivar
Height		
Allometrically adjusted height		
Height FRic		
Height Rao's Q		
SLA	0.042	
SLA FRic		
SLA Rao's Q		
LDMC	0.053	
LDMC FRic		
LDMC Rao's Q		

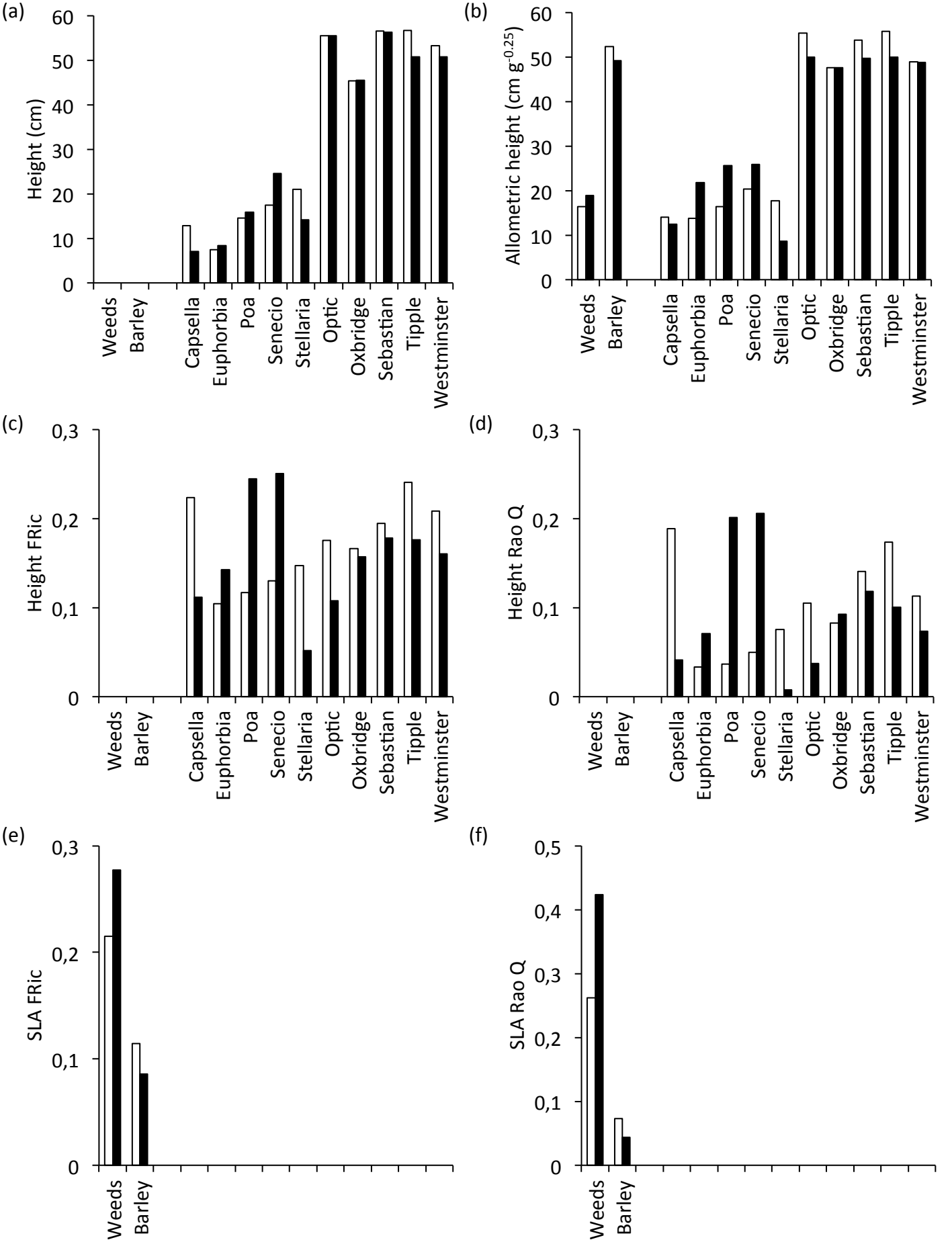
674 Fig. 1. Impact of diversity (□ taxa grown alone, ■ taxa grown in a five taxa mixture, either
675 five weed species or five barley cultivars) on the traits and functional diversity of individual
676 barley cultivars and weed species on the taxa groups (weeds, barley, H1) or on the
677 individual taxa (H1b). Bars shown only if the statistical test is significant: (a) Height (cm), (b)
678 allometrically adjusted height (cm $g^{-0.25}$), (c) Functional richness of height, (d) Rao's Q of
679 height, (e) Functional richness of SLA (Specific Leaf Area), and (f) Rao's Q of SLA. Errors bars
680 represent 1 s.e.
681
682

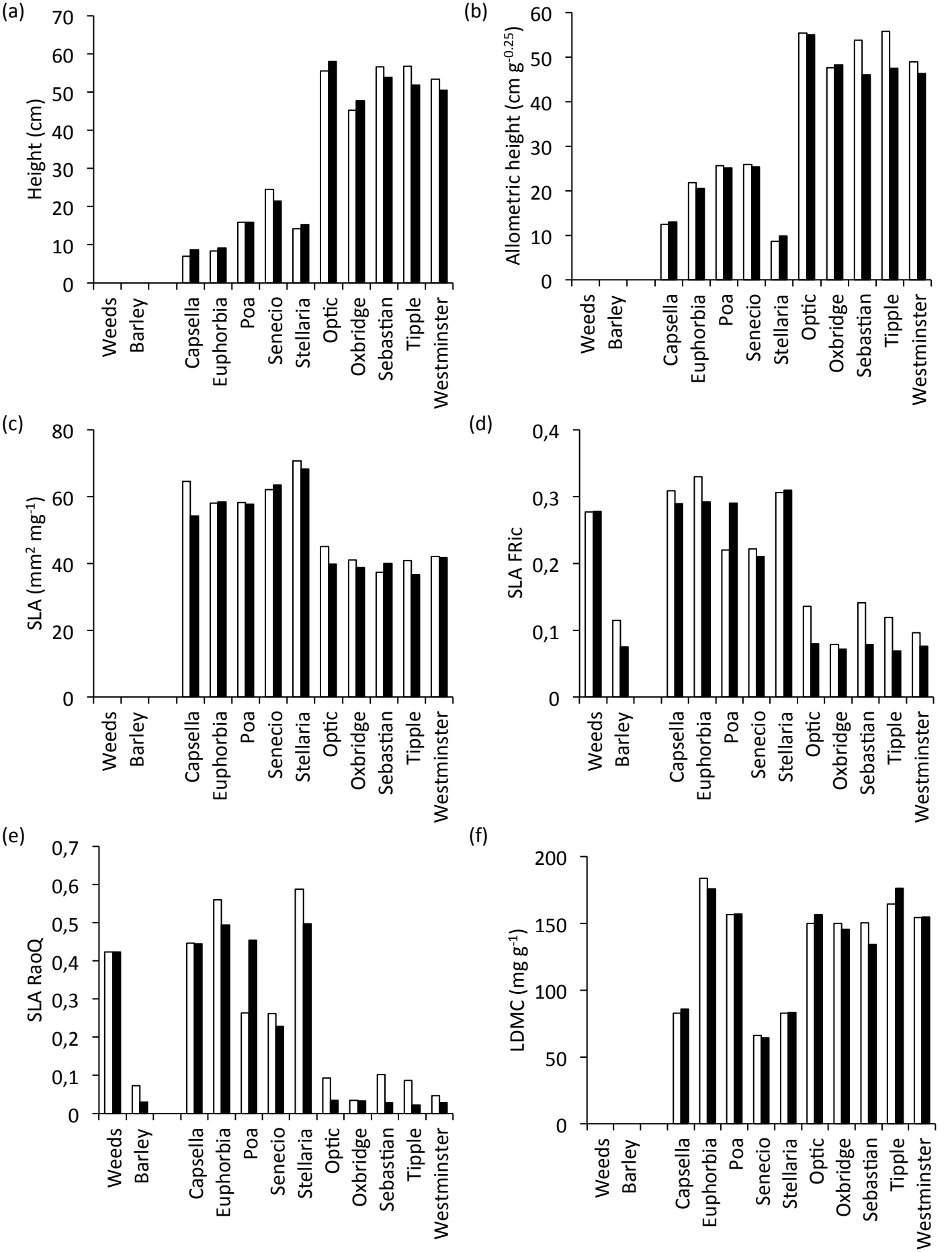
683 Fig. 2. Impact of growing in crop-weed mixtures (□ taxa grown alone, ■ taxa grown in crop-
684 weed mixture) on the traits and functional diversity of the taxa groups (weeds, barley, H2)
685 or on the individual barley cultivars and the weed species (H2b): (a) Height (cm), (b)
686 allometrically adjusted height (cm $g^{-0.25}$), (c) SLA (Specific Leaf Area, mm^2 mg^{-1}), (d)
687 Functional richness of SLA, (e) Rao's Q of SLA, and (f) LDMC (Leaf Dry Matter Content, mg g^{-1}
688). Errors bars represent 1 s.e.
689
690

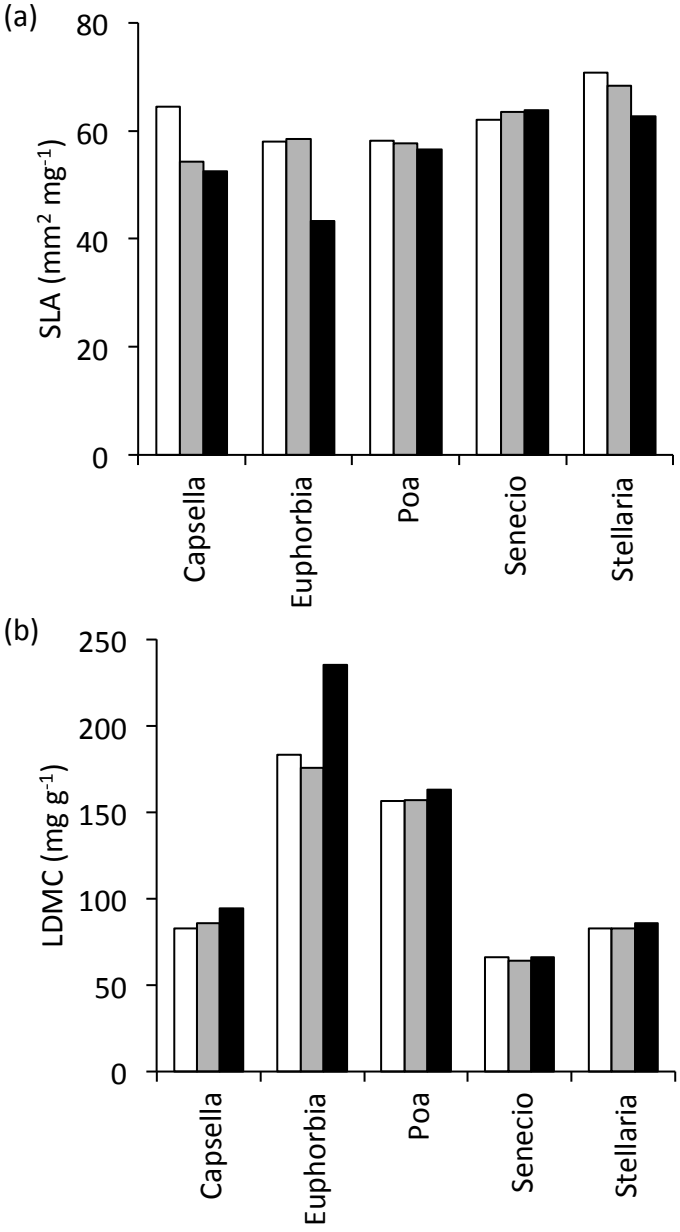
691 Fig. 3. Impact of increasing barley cultivar richness (□ no barley, ■ mean of single barley
692 cultivars, ■ five barley mixtures) on individual weed species traits: (a) SLA (Specific Leaf
693 Area, $mm^2\ mg^{-1}$), and (b) LDMC (Leaf Dry Matter Content, $mg\ g^{-1}$). Errors bars represent 1
694 s.e.
695
696

697 Fig. 4. Impact of growing with weeds (□ no weeds present, ■ weeds present), overall (H4)
698 and on the five individual barley cultivars and the five cultivar mixture (H4b): (a)
699 allometrically adjusted height (cm $g^{-0.25}$), (b) SLA (Specific Leaf Area, mm^2 mg^{-1}) and (c) Rao's
700 Q of SLA. Errors bars represent 1 s.e.
701
702

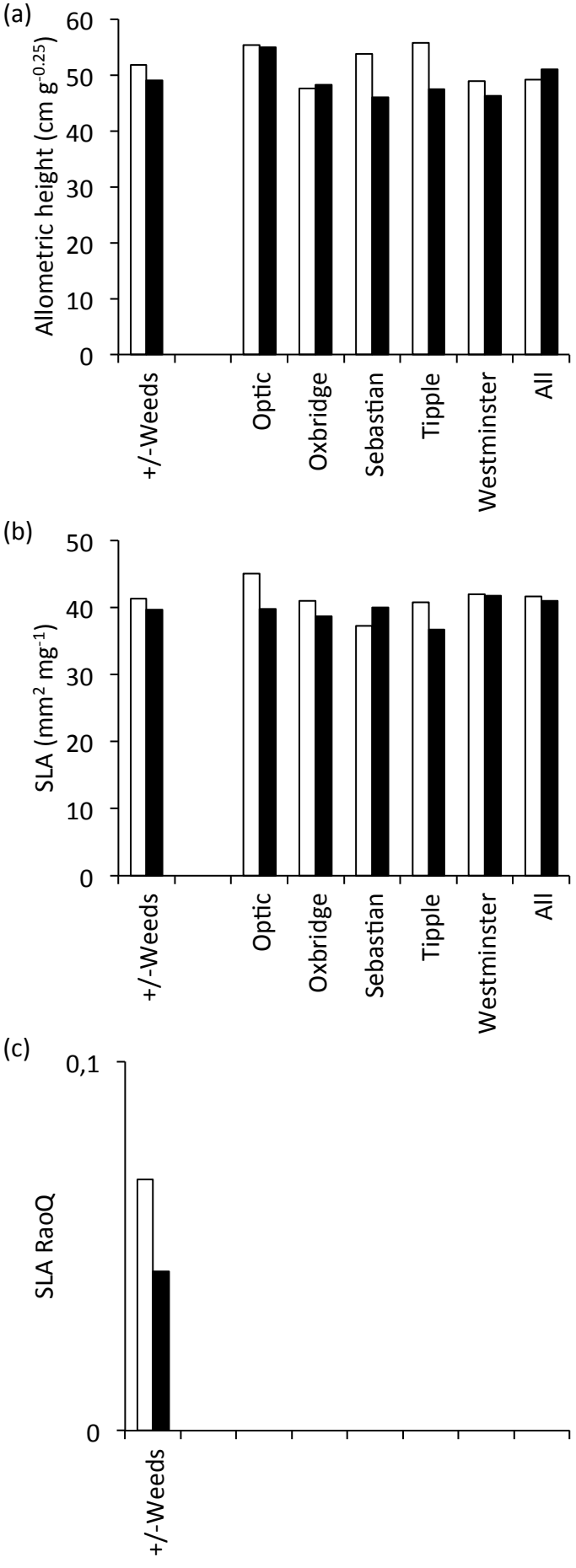
703 Fig. 5. Impact of increasing barley cultivar richness (□ no barley, ■ mean of single barley
704 cultivars, ■ five barley mixtures) on the weighted mean traits of the whole weed
705 community: (a) SLA (Specific Leaf Area, $mm^2\ mg^{-1}$) and (b) LDMC (Leaf Dry Matter Content,
706 $mg\ g^{-1}$). Errors bars represent 1 s.e.
707
708

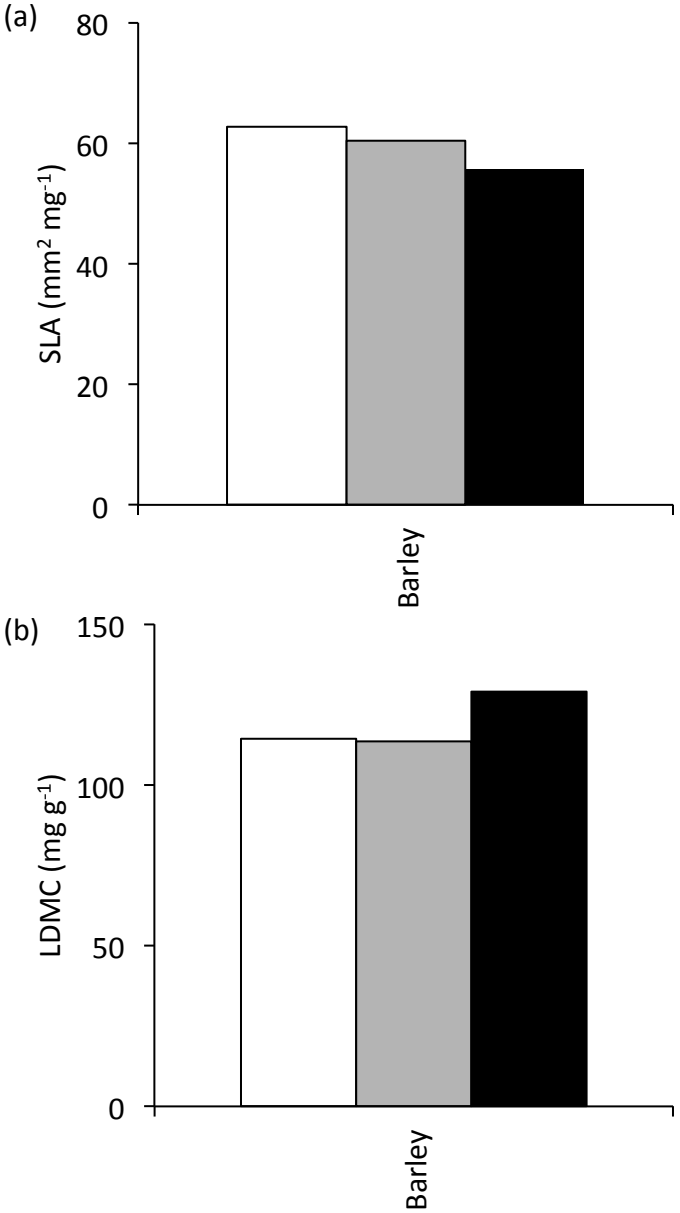

(a)
Height (cm)
0
10
20
30
40
50
60
Weeds
Barley
Capsella
Euphorbia
Poa
Senecio
Stellaria
Optic
Oxbridge
Sebastian
Tipple
Westminster
(b)
Allometric height (cm g-0.25)
0
10
20
30
40
50
60
Weeds
Barley
Capsella
Euphorbia
Poa
Senecio
Stellaria
Optic
Oxbridge
Sebastian
Tipple
Westminster
(c)
Height FRic
0
0,1
0,2
0,3
Weeds
Barley
Capsella
Euphorbia
Poa
Senecio
Stellaria
Optic
Oxbridge
Sebastian
Tipple
Westminster
(d)
Height Rao Q
0
0,1
0,2
0,3
Weeds
Barley
Capsella
Euphorbia
Poa
Senecio
Stellaria
Optic
Oxbridge
Sebastian
Tipple
Westminster
(e)
SLA FRic
0
0,1
0,2
0,3
Weeds
Barley
(f)
SLA Rao Q
0
0,1
0,2
0,3
0,4
0,5
Weeds
Barley


(a)
Height (cm)
0
10
20
30
40
50
60
70
Weeds
Barley
Capsella
Euphorbia
Poa
Senecio
Stellaria
Optic
Oxbridge
Sebastian
Tipple
Westminster
(b)
Allometric height (cm g-0.25)
0
10
20
30
40
50
60
Weeds
Barley
Capsella
Euphorbia
Poa
Senecio
Stellaria
Optic
Oxbridge
Sebastian
Tipple
Westminster
(c)
SLA (mm2 mg-1)
0
20
40
60
80
Weeds
Barley
Capsella
Euphorbia
Poa
Senecio
Stellaria
Optic
Oxbridge
Sebastian
Tipple
Westminster
(d)
SLA FRic
0
0,1
0,2
0,3
0,4
Weeds
Barley
Capsella
Euphorbia
Poa
Senecio
Stellaria
Optic
Oxbridge
Sebastian
Tipple
Westminster
(e)
SLA RaoQ
0
0,1
0,2
0,3
0,4
0,5
0,6
0,7
Weeds
Barley
Capsella
Euphorbia
Poa
Senecio
Stellaria
Optic
Oxbridge
Sebastian
Tipple
Westminster
(f)
LDMC (mg g-1)
0
50
100
150
200
Weeds
Barley
Capsella
Euphorbia
Poa
Senecio
Stellaria
Optic
Oxbridge
Sebastian
Tipple
Westminster


(a)
80
60
40
20
0
SLA (mm² mg⁻¹)
Capsella
Euphorbia
Poa
Senecio
Stellaria

(b)
250
200
150
100
50
0
LDMC (mg g⁻¹)
Capsella
Euphorbia
Poa
Senecio
Stellaria


(a)
Allometric height (cm g-0.25)
60
50
40
30
20
10
0
+/-Weeds
Optic
Oxbridge
Sebastian
Tipple
Westminster
All
(b)
SLA (mm2 mg-1)
50
40
30
20
10
0
+/-Weeds
Optic
Oxbridge
Sebastian
Tipple
Westminster
All
(c)
SLA RaoQ
0,1
0
+/-Weeds


(a)
80
60
40
20
0
SLA (mm² mg⁻¹)
Barley

(b)
150
100
50
0
LDMC (mg g⁻¹)
Barley